Webs in vitro and in vivo: spiders alter their orb-web spinning behavior in the laboratory

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Abstract.   Many studies of the elegant architectures of orb webs are conducted in controlled laboratory environments that remove environmental variability. The degree to which spider behavior in these circumstances resembles that of spiders in the wild is largely unknown. We compared web architecture and silk investment of furrowed orb weavers *Larinioides cornutus* (Clerck 1757) building webs in laboratory cages and spinning webs on fences in the field and found significant differences. The volume of major ampullate silk in radii was 53% lower in cage webs, primarily because the silk was 50% thinner, but also because spiders tended to spin 14% fewer radii than in fence webs. Cage spiders also invested about 40% less flagelliform silk and aggregate glue in the capture spiral, although the difference was not statistically significant, a trend primarily driven by a decrease in the length of the glue-coated capture spiral. These patterns were consistent with spiders reducing silk investment when building at new web sites while they assessed insect abundance. Differences in the type of substrate for web attachment, amount of available space, and condition may also have influenced web architecture. Cage webs were more symmetrical than fence webs, which displayed an unusual horizontal asymmetry that may have maximized their capture areas within the constraints of the available fence-railing attachment sites. Our findings suggest using caution when generalizing the properties of laboratory-spun webs to more natural conditions. More importantly, they demonstrate that orb spiders actively modify their behaviors when spinning webs under different conditions.

Keywords: Foraging, silk investment, behavioral plasticity, silk thread size, web architecture

The silk that orb spiders invest in webs is critical for determining energetic gain through captured insect prey (Sherman 1994; Blackledge & Eliason 2007). Therefore, the rich variation in sizes and shapes of orb webs among different species of spiders may potentially be explained by the relative costs and benefits of silk investment and web architecture for particular environments (Shear 1986; Eberhard 1990; Higgins 1995). For instance, spiders should invest more silk in environments that are least likely to damage the web or that are most likely to yield prey (Higgins & Buskirk 1992; Blackledge & Wenzel 2001; Segoli et al. 2004). Spiders modify web-spinning behavior in response to environmental factors that include wind (Eberhard 1971; Henschel & Lubin 1992), prey abundance (Pasquet et al. 1994; Higgins 1995; Blackledge 1998; Herberstein et al. 2000; Blackledge & Zevenbergen 2007), prey taxon (Sandoval 1994; Tso et al. 2007), competition with other individuals (Leborgne & Pasquet 1987; Ward & Lubin 1992), frequency of damage by non-prey animals (Chmiel et al. 2000), and size of the vegetation scaffold on which the web is constructed (Lubin et al. 1991). Typically, such studies document changes in specific web properties including size of the capture area as well as the total length or spacing of threads, and then attempt to relate these changes to foraging investment under different environmental conditions.

However, accurately assessing foraging investment is difficult, as it may be possible to divert available silk resources in multiple ways to achieve equivalent foraging success. For example, a web with closely spaced threads is very good at stopping and retaining large insects, but a larger web increases the number of interceptions (Eberhard 1986; ap Rhisiart & Vollrath 1994; Nakata & Ushimaru 2004; Blackledge & Eliason 2007). For a given volume of silk, thick, high energy

absorbing threads necessarily trade off with large capture area or a fine mesh width. The important role of tradeoffs between web architecture and silk structure has largely been ignored by studies that focus solely on changes in web architecture, which represent almost all previous work in this area (e.g. Sherman 1994; Herberstein et al. 1997; Nakata & Ushimaru 1999; Heiling & Herberstein 2000; Nakata 2007).

Orb webs are spun largely using two very different types of fibrous silk. The potential for a web to stop the flight of different insects depends on the amount and placement of each silk within the web. Spiders first produce an outer framework and supporting radial threads using dry dragline silk from the major ampullate (MA) silk glands (Foelix 1996). They then spin a spiral of elastic, adhesive silk onto the radial threads using a combination of fibrous flagelliform (Flag) silk and gluey aggregate (Ag) silk (Foelix 1996). Together these different silks compose a planar orb (Fig. 1) that functions in first intercepting insects, then absorbing the kinetic energy of their flight, and finally adhering to the insects long enough for the spider to capture them (Blackledge & Hayashi 2006).

Many studies of orb webs are based on laboratory-confined spiders due to experimental convenience and control over the environment (Zschokke & Herberstein 2005). However, such spiders spin webs in an environment that is fundamentally different from their natural habitat. This could potentially influence many features of webs (Brown 1981; Gillespie & Caraco 1987; Higgins et al. 2001). Here, we compare the difference in web investment between spiders spinning in an outdoor setting along fence railings that impose size constraints on webs but is otherwise natural and a laboratory environment that imposes not just size constraints but also changes in prey cues, web supports and weather, using the furrowed orb spider *Larionioides cornutus* (Clerck 1757) (Araneae: Araneidae). We test the prediction that the

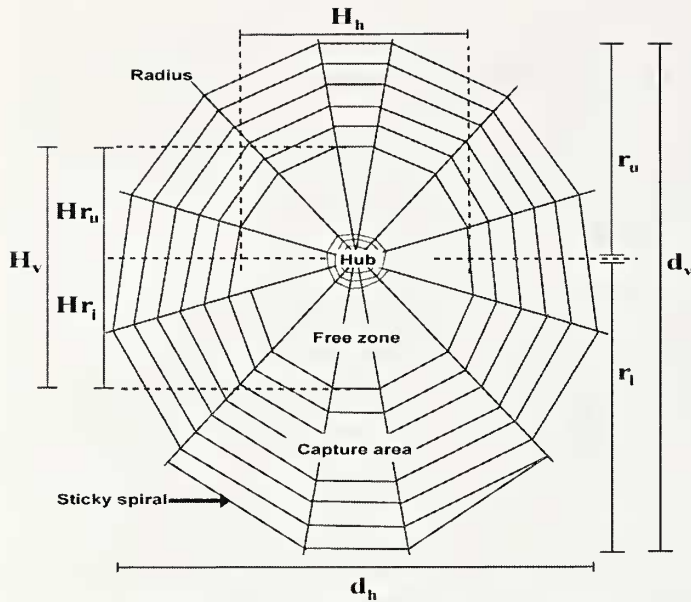[3]Corresponding author. E-mail: andrew6@uakron.edu

Figure 1.—Web architecture parameters measured: Vertical diameter (d_v) of the capture area, horizontal diameter of the capture area (d_h), upper radial length (r_u), lower radial length (r_l), upper free zone length (Hr_u), lower free zone length (Hr_l), free zone vertical diameter (H_v), and free zone horizontal diameter (H_h). Capture area is delimited by the outermost sticky spirals.

laboratory environment will affect silk investment and web architecture and find that some measures of investment are reduced in the laboratory environment.

METHODS

Study species.—We compared silk investment and architecture of webs spun by a single population of *L. cornutus* in the field versus laboratory. *L. cornutus* is a common nocturnal orb-weaving spider, a cosmopolitan species known for building webs above or near water, particularly on human-made structures such as bridges (Burgess & Uetz 1982; see also Heiling 1999; Heiling & Herberstein 1999). These spiders often spin webs at unusually high population densities for orb-weaving spiders. All of the spiders in this study came from a 100-m long bridge over the Cuyahoga River in Akron, Summit County, Ohio, USA. Multiple generations of spiders coexisted, and webs were in close proximity but not interconnected. These spiders usually initiate web construction at dusk and then hunt at the hub during the night while remaining in a retreat located above or to the side of the web during daylight.

Fence spiders.—We sampled the webs of 11 sexually mature females [132 ± 64 mg, (mean ± SD) and 4.3 ± 0.6 mm carapace length] on the fence railings of the bridge in August and September 2008. This population was also the source of the specimens used for the cage treatment. Fence webs were spun between the vertical confines of wooden railings, 18–25 cm apart; or metal railings, 23–24 cm apart (Fig. 2). Spiders were collected from the webs and web measurements made between 21:00 and 23:00 h, shortly after webs were spun. We recognized freshly spun webs by their intact spirals and radial spokes as well as the lack of insects or detritus.

Caged spiders.—Thirteen sexually mature female *L. cornutus* (131 mg ± 63 mg and 4.7 mm ± 0.6 mm carapace length) were captured in August 2007, placed in cages measuring 40 × 40 × 10 cm in the laboratory, and allowed to spin webs (Agnarsson & Blackledge 2009). The cages were composed of metal frames, with clear plexiglass on the 40 × 40 cm faces, and insect screen on the remaining four 10-cm-wide edges. Spiders experienced minimal temperature variation (22 ± 3 °C), airflow and insect cues, as well as a constant 15:9 h L:D cycle in the laboratory. The cages also provided stiff vertical supports for the sides of webs, which were generally lacking for one or both sides of fence webs. Spiders typically constructed webs within 1–5 days of captivity and were not fed prior to web spinning.

Fence ($n = 11$) and caged spiders ($n = 13$) were equivalent in body mass and carapace width but differed in body
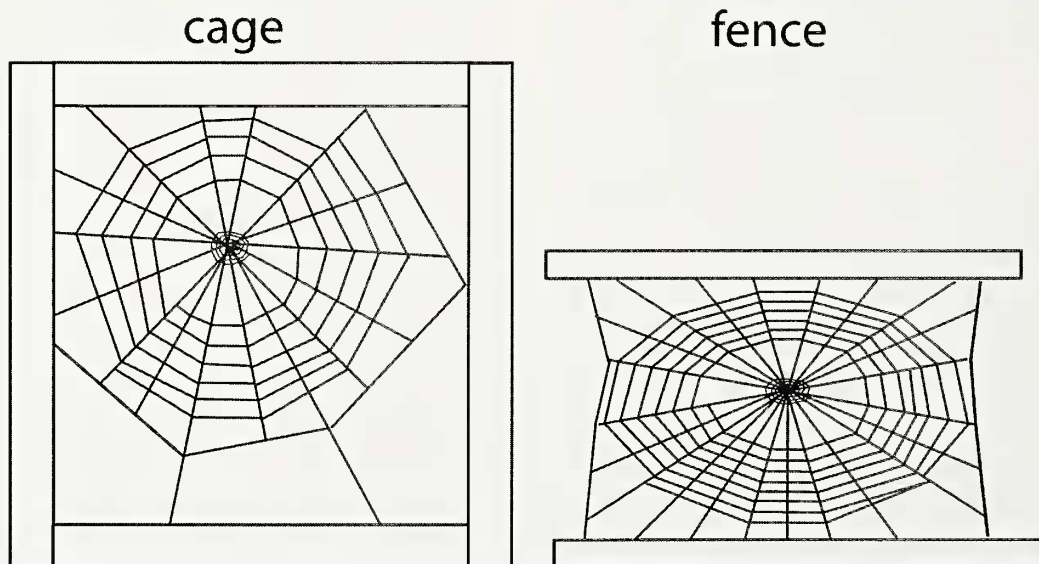
cage

fence

Figure 2.—Sketch summarizing the important differences between cage and fence webs. The relative sizes of the substrates reflect the different shapes of space available to spiders in the laboratory and field. Cages measured 40 × 40 × 10 cm, while fence railings were separated by 18–25 cm but allowed semi-unconstrained widths of webs. Only 1/3 of the typical spiral threads are shown, but radii count is similar to real webs.

Table 1.—Body parameters (median, minimum, maximum) of spiders used in the cage ($n = 13$) and fence ($n = 11$) web comparisons. Weight and carapace width did not differ in median between cage and fence spiders (Mann-Whitney U test by ranks, $P = 1.00$ and $P = 0.28$, respectively). Body condition was significantly lower in cage spiders (Mann-Whitney U test by ranks, $P = 0.01$).

	Cage spiders (median, min, max)	Fence spiders (median, min, max)
Weight (mg)	102, 64, 265	117, 42, 213
Carapace width (mm)	3.7, 3.2, 5	3.6, 2.6, 4.1
Body condition	−0.12, −0.33, 0.27	0.07, −0.07, 0.16

condition, with fence spiders having higher body condition (Table 1). For each spider, we measured aspects of silk structure and orb-web architecture that played potentially critical roles in prey capture and allowed quantification of total silk investment by spiders.

Web architecture measurements.—For caged spiders, web architecture was measured from digital photographs taken from webs placed in front of a shadow box and illuminated from the sides by fluorescent lighting (Langer & Eberhard 1969; Zschokke & Herberstein 2005). For fenced spiders, it was difficult to obtain clear photographs of entire webs so that architecture was instead measured directly in the field using techniques described by Blackledge et al. (2003). For both types of webs, we measured the vertical diameter of the capture area (d_v), horizontal diameter of the capture area (d_h), upper radial length (r_u), lower radial length (r_l), upper free zone length (Hr_u), lower free zone length (Hr_l), free zone vertical diameter (H_v), and free zone horizontal diameter (H_h) (Fig. 1).

Capture area is delimited by the outermost sticky spirals and determines the number of insects that a web potentially intercepts. Capture area was measured directly from photographs of laboratory webs using Image J (Rasband 1997–2009) and was calculated for field webs using the Adjusted Radii-Hub formula (Blackledge & Gillespie 2002):

$$\text{Capture area} = \left[\frac{1}{2}\pi \, r_{au}^2 - \frac{1}{2}\pi (Hr_u)^2 \right] + \left[\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi (Hr_l)^2 \right],$$

where $r_{au} = (r_u + d_h/2)/2$ and $r_{al} = (r_l + -d_h/2)/2$.

The density of threads within webs influences the sizes of insects likely to be intercepted, but more importantly affects both the ability of webs to absorb the kinetic energy of flying insects and whether webs retain insects long enough to be captured by spiders (Blackledge & Zevenbergen 2006). Therefore we counted the number of radii and the number of spiral threads along four axes (top, bottom, left, and right). Mesh width, the distance between adjacent capture spirals, was calculated along each axis and then averaged (Herberstein & Tso 2000).

Spiders usually place the web hub above the center of the orb, resulting in a web with a larger lower capture region (Krink & Vollrath 1997, 2000). This hub asymmetry typically increases with spider size (Kuntner et al. 2008) and is

hypothesized to decrease the time necessary for a heavy spider to reach an insect caught in the lower catch region (Masters & Moffet 1983; Nentwig 1985; Herberstein & Heiling 1999; Heiling 2004). Alternately, the larger lower capture area may reduce the high metabolic cost of raising the abdomen above the body when spiders spin the capture spiral in the upper region of the web (Herberstein & Heiling 1999). Hub asymmetry is defined in Blackledge & Gillespie (2002) as:

$$\text{Hub asymmetry} = 1 - r_u/r_l.$$

Most orb webs are not round, but rather elliptical. The exaggerated vertical axis of webs may facilitate prey capture by taking advantage of the tendency of prey to tumble downward as they struggle. Web asymmetry describes the relationship between height and width of the orb and is defined in Blackledge & Gillespie (2002) as:

$$\text{Web asymmetry} = 1 - d_h/d_v.$$

Perfectly round webs have a web asymmetry value of 0. A web asymmetry < 0 indicates a web that is wider than it is tall, and web asymmetry > 0 indicates a web that is taller than wide.

Silk structure.—Finally, investment of silk in a web can be quantified by measuring the structural sizes of threads and glue droplets. For each web, four radial threads, one from each cardinal axis, were collected onto cardboard holders described in Agnarsson & Blackledge (2009). Cyanoacrylate adhesive (Superglue™) was applied to two sides of a 16 mm hole in the center of the card, which was then pressed against a radius. After drying for several seconds, the radial thread was cut on either end of the card using a portable soldering iron, releasing the thread from the web.

To measure spiral thread diameter, the silk was collected directly onto a glass microscope slide by placing the slide behind the four outermost strands and then gently pressing the slide against the web. The spiral threads were then cut along the edges of the slide with a portable soldering iron. The glass slide caused the glue droplets to adhere and flatten, thereby securing the threads to the slide and making the core axial thread visible. We used the same procedure as Agnarsson & Blackledge (2009) and Blackledge et al. (2005) to measure radial and spiral thread diameters using polarized light microscopy at 1000× magnification.

Total volume of flagelliform silk in the capture spiral was calculated by first determining the total length of the capture spiral, typically designated as capture thread length (CTL) (Sherman 1994):

$$\text{CTL} = \pi \, (\text{average \# spirals along the 4 web axes}) \\ [(r_u + d_h + r_l)/4 - (Hr_u + H_h + Hr_l)/4].$$

The factor in the brackets represents the average width of the capture area and is estimated by subtracting the average free zone radius along the four cardinal axes from the average capture area radius along the four cardinal axes.

Volume was then computed as:

$$\text{total spiral thread volume} = (\text{CTL}) \, \pi \, (\text{hypothetical spiral diameter}/2)^2.$$

The diameter of a hypothetical thread that would be equivalent in cross-sectional area to the two strands of

spiral fibers that typically compose capture spirals was calculated as:

$$\text{hypothetical spiral thread diameter} = 2 \left[2\pi\, r_{ss}^2 \right]^{0.5} / \pi,$$

where r_{ss} was the measured radius of a single strand, assuming equal radius of each strand. Hypothetical radial thread diameter was calculated in an identical manner, also assuming that the radial thread was composed of two equally sized strands. In the rare instances in which we observed four-stranded radial or capture threads, all four strands were assumed to be of equal diameter, and a factor of $\sqrt{2}$ was included in the hypothetical thread diameter formula shown above. The average hypothetical thread diameter for a specific web and specific silk type was then calculated as the average of the four collected thread samples.

Total radial thread volume was calculated as:

Total radial thread volume
= (average single radial length)
(# radial threads)(average cross-section area)
= $(r_u + d_h + r_u)/4$ (radii count)
π (hypothetical radial thread diameter/2)^2.

To measure glue droplet volume on the capture spiral silk, we suspended threads between 3 mm diameter wooden supports secured to a microscope slide. The four outermost capture spiral rows, adjacent to those already captured by direct adhesion to glass, were collected simultaneously by pressing this slide against the web so that the threads bridged the gap between the parallel supports (Agnarsson & Blackledge 2009). Glue droplets were photographed at 10 or 100× magnification, and the length and width of the first and third droplet from the left edge of the photo were measured. This avoided experimenter bias toward measuring large or small droplets. We did not measure the much smaller secondary droplets that often occur between primary droplets because secondary droplets contribute minimally to total glue volume (Opell & Hendricks 2007). The volume of a single droplet of glue (SDV) was calculated as:

$$\text{SDV} = (\text{droplet width})^2 (\text{droplet length})/15.$$

This formula accounts for the anisotropy of the droplet shape, which tends to be longer than wide as it adheres to the spiral thread (Opell et al. 2008). The average distance between glue droplets was measured across 10 adjacent droplets. Total volume of glue within the web was then calculated as:

Total glue volume =
(SDV)(CTL)/average distance between droplets.

Droplet size can increase with the relative humidity of the air due to the hygroscopicity of glue silk (Mark et al. 1991; Opell & Schwend 2008). Laboratory relative humidity was between 40–60% R.H. during measurement of all threads and thus was lower than the occasional high humidity (90%) that occurred in the field. For all spiders, droplets were measured within approximately 2 h of collection, and hence 2–4 h after web production, to minimize any effect of drying or swelling on droplet volume.

STATISTICAL METHODS

Comparing spider body condition.—Because spiders were collected from the same bridge on consecutive years in autumn, we first determined whether the spiders from fence webs and cage webs differed in body size or condition. Body condition was calculated as the residuals of the regression of log weight onto log carapace width (Table 1) (Jakob et al. 1996). Mann-Whitney U tests were used to test for differences between weight, carapace width, and spider body condition, because these variables were not normally distributed. These tests found that spiders collected from fence and cage webs did not differ in weight ($P = 1.00$) or carapace width ($P = 0.28$), but did differ in body condition ($P = 0.02$), with fence spiders having higher body condition (Table 1). The most likely reason for this difference is that the cohort associated with each year experienced slightly different foraging histories. Thus, location is confounded with body condition, so that some differences between fence and cage webs could be due to difference in body condition.

Comparing webs.—The effect of captivity on web architecture was then tested using Multivariate Analysis of Variance (MANOVA) implemented in Statistica 6.1. We included 13 variables in the model (Table 2). Cross-sectional area of radial (MA) and spiral (Flag) threads, volume of capture silk, volume of glue, and glue droplet spacing were log transformed to meet assumptions of the normal distribution (Shapiro-Wilks W test, $P > 0.05$) and homogeneous variance (Levene's Test for Homogeneity of Variances, $P > 0.05$). Radial volume was transformed by a power exponent of 0.25 to achieve normality. Radii number and web asymmetry were normally distributed but could not be successfully transformed to achieve homogenous variance between cage and fence webs. There is no readily available non-parametric equivalent to MANOVA, hence the MANOVA was also performed without these two variables to confirm that their inclusion did not affect the results. Post-hoc unequal n honest significant difference (HSD) mean comparison tests were used to detect which variable means differed between webs on fences and in cages. Because radial count and web asymmetry did not satisfy all assumptions of parametric tests, and radial volume did so only marginally even after transformation, we also performed univariate Mann-Whitney U tests by ranks for these three variables as raw variables.

RESULTS

There was a significant difference in web properties between cage and fence spiders (MANOVA, Wilks $\Gamma = 0.052$, $F_{13, 6} = 8.37$, $P = 0.008$). Unequal n HSD tests indicated that laboratory webs had shorter CTL ($P = 0.008$) (Fig. 3D), smaller radial cross-sectional area ($P = 0.03$), and lower asymmetry ($P = 0.006$) than field webs (Table 2). The significant effect of web location in the overall model and the significant post-hoc mean differences of CTL and radial cross-sectional area were not changed by excluding the non-parametric variables, web asymmetry and radial count, from the MANOVA model.

The univariate Mann-Whitney U tests identified lower median web asymmetry in fence webs (fence median -0.27, range -0.8 to 0.5, cage median 0.11, range -0.18 to 0.4, Mann-Whitney $U = 19$, $P = 0.003$, Fig. 3G). The Mann-

Table 2.—Web architecture (mean ± SD, n) compared between cage and fence spiders. For the variables that met the normal distribution and homogeneous variance assumptions of MANOVA, significant post-hoc unequal n HSD mean differences between cage and field are indicated with a * ($P < 0.05$). Significant median differences identified by the Mann-Whitney U tests are indicated with a † ($P < 0.05$). Sample size for the glue measurements was smaller than for the other samples due to accidental destruction prior to measurement. Capture thread length is abbreviated as CTL.

	Cage webs	Fence webs	% difference
Web architecture			
Capture area (cm²)	462 ± 213 (13)	593 ± 247 (11)	22
Number of radii	17.8 ± 2.0 (13)	21 ± 3.2 (11)	14†
CTL (cm)	555 ± 217 (13)	963 ± 277 (11)	42*†
Mesh width (mm)	4.6 ± 0.8 (13)	4.2 ± 0.8 (11)	−10
Web asymmetry	0.1 ± 0.1 (13)	−0.3 ± 0.3 (11)	136†
Hub asymmetry	0.3 ± 0.2 (13)	0.2 ± 0.2 (11)	−50
Silk structure			
Radial (MA) cross-section area(μm²)	5.6 ± 3.6 (13)	11.3 ± 5.8 (11)	50*†
Capture spiral (Flag) cross-section area (μm²)	6.7 ± 1.9 (13)	4.5 ± 1.0 (11)	−33
Glue single drop vol.(μm³)	7087 ± 5062 (12)	7800 ± 5592 (8)	10
# glue droplets/mm	17 ± 6 (12)	16 ± 6 (9)	−8
Silk investment			
Radial volume (mm³)	0.016 ± 0.008 (13)	0.034 ± 0.019 (11)	53†
Spiral volume (mm³)	0.026 ± 0.020 (13)	0.045 ± 0.029 (11)	41
Glue volume (mm³)	0.6 ± 0.5 (12)	1.0 ± 0.7 (8)	38

Whitney U tests also identified a greater median number of radii in fence webs (fence median 22, range 15–25, cage median 18, range 15–22, Mann-Whitney $U = 35$, $P = 0.037$, Fig. 3B) and greater median radial volume in fence webs (fence median 0.033 mm³, range 0.006 to 0.07, cage median 0.013 mm³, range 0.004–0.03, Mann-Whitney $U = 28$, $P = 0.01$, Fig. 3C, Table 2, Fig. 4A). Because of the non-homogeneous and marginally homogeneous variance of these two variables (Levene's Test for Homogeneity of Variances, $P = 0.03$, $P = 0.08$), respectively, the Mann-Whitney U tests may have offered greater power to reject the null hypothesis than the MANOVA.

DISCUSSION

Most research on energetic investment associated with construction of orb webs focuses on total thread length (e.g. Turnbull 1964; Nakata & Ushimaru 2004; Kawamoto & Japyassu 2008). However, this ignores the important contribution of thread diameter to web function and total silk investment. Our study quantifies this potentially important parameter and directly compares web architecture and silk investment between fence and cage webs to gain a more accurate estimate of the material investment of spiders in webs. On average, cage webs were smaller and rounder than fence webs, contained shorter lengths of capture spirals, and were supported by fewer, as well as thinner, radii. Thus, spiders invested significantly less radial (MA) silk in the cage webs. There was also a consistent, albeit non-significant, trend toward lower volumes of flagelliform capture spiral silk (Flag) and aggregate glue (Ag). These differences suggest that spiders may initially reduce silk investment in webs when moved into cages. However, several other factors, particularly spider condition, cohort, and available web frame size may also contribute to the observed differences in investment. These factors were confounded with the transition from fence to

cage. Our study primarily addresses the concerted changes of silk and web architecture. Secondarily, we speculate on the adaptive significance of those changes.

Decreased investment in silk likely has implications for web performance. In other web systems, recent investigations of the tradeoffs inherent in modifying web architectures revealed that the effective capture of larger prey depends more upon the increased energy absorption and stickinesss supplied by a concentrated capture spiral than on increased capture area (Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007). High capture area remains, however, as an effective strategy of increasing interception rate of all prey sizes and successful capture of small prey. Larger mesh width, in conjunction with greater capture area, has been reported as a typical response to larger prey (Herberstein & Heiling 1998; Schneider & Vollrath 1998). However, all of these studies largely assume that size and mechanical properties of silk threads are invariant in different spinning scenarios. We show here that, at least in this species, the common simplification of invariant thread size is not valid for radial threads, but the data are consistent with bigger webs as "better" webs. For *L. cornutus* caged webs, the reduced capture area, increased mesh width, and decreased silk volume all predict that these webs should function poorly at intercepting, stopping and retaining prey compared to field webs. The reduction of radial thread cross-sectional area in *L. cornutus* caged webs thus accompanies the reduction in many other parameters associated with high prey energy absorption, suggesting a concerted decline in web investment rather than a compensatory effect.

Spiders in laboratory cages built architecturally different webs from those on fences. Such shape variation may result in part from the reduced silk investment in cage webs, but also likely relates to the characteristics of the available supports for webs in cages versus fences. In both environments, web spinning was constrained by the rigid dimensions of the
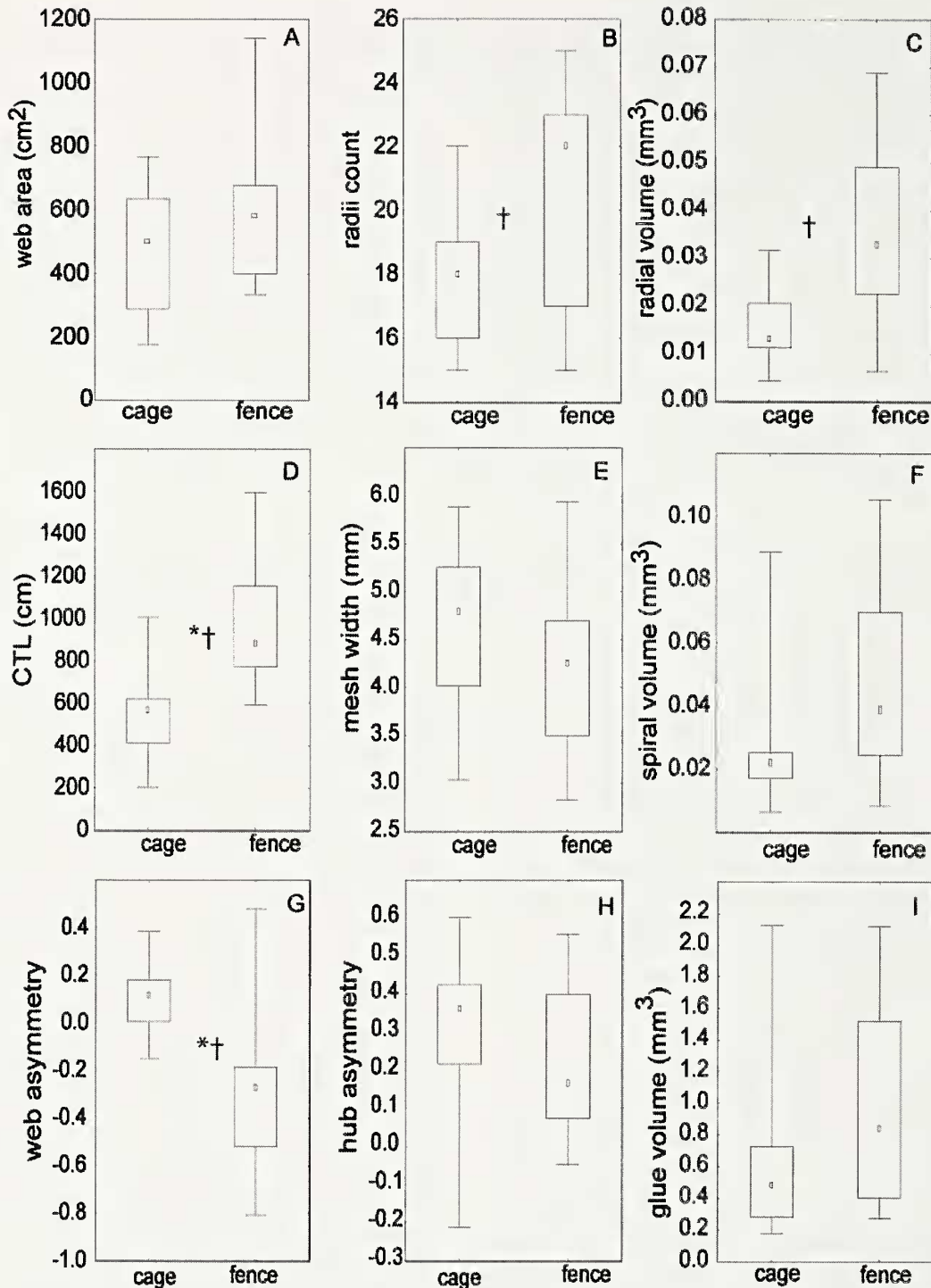
Figure 3.—Web architecture and silk investment in laboratory cage and fence webs (median indicated by small box, 25–75 percentiles indicated by large box, and range indicated by capped bars). Non-parametric values of median, minimum, and maximum are shown because the parametric parameters of mean and standard deviation are presented in Table 2. Statistically significant differences in MANOVA post-hoc unequal n HSD tests are indicated by * ($P < 0.05$). Significant median differences identified by the Mann-Whitney U tests are indicated with a † ($P < 0.05$). A. Capture area (MANOVA post-hoc unequal n HSD test, $P = 0.52$); B. Number of radii (Mann-Whitney $U = 35$, $P = 0.037$); C. Radial volume (Mann-Whitney $U = 35$, $P = 0.037$); D. Capture thread length, CTL (MANOVA post-hoc unequal n HSD test, $P = 0.008$); E. Mesh width (MANOVA post-hoc unequal n HSD test, $P = 0.21$); F. Total spiral volume (MANOVA post-hoc unequal n HSD test, $P = 0.31$); G. Web asymmetry (Mann-Whitney $U = 19$, $P = 0.003$); H. Hub asymmetry (MANOVA post-hoc unequal n HSD test, $P = 0.13$); I. Total glue volume (MANOVA post-hoc unequal n HSD test, $P = 0.18$).
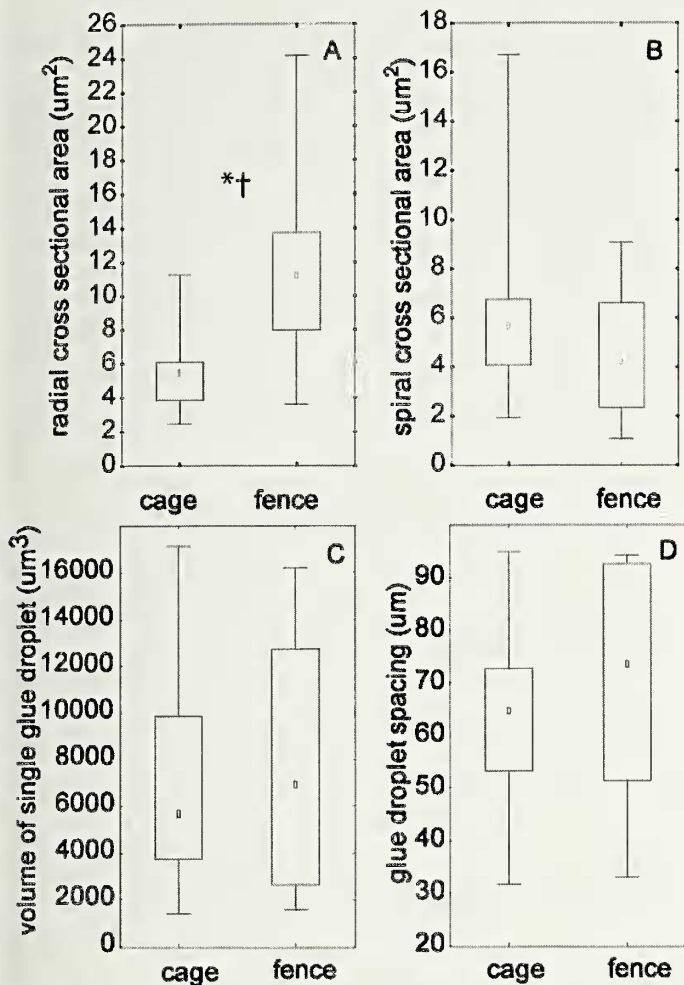
Figure 4.—Thread properties of cage and fence webs (median indicated by small box, 25–75 percentiles indicated by large box, and range indicated by capped bars). Statistically significant differences in MANOVA post-hoc unequal n HSD test indicated by *($P < 0.05$). Significant median differences identified by the Mann-Whitney U tests are indicated with a † ($P < 0.05$). A. Radial cross sectional area of the double-stranded radial (MA) fiber ($P = 0.03$); B. Spiral cross-sectional area of the double-stranded capture (Flag) fiber ($P = 0.74$); C. Single glue droplet volume ($P = 0.79$); D. Glue droplet spacing ($P = 0.77$).

surroundings. Cage spiders could, and did, attach frame threads above, below, and to either side of the web, resulting in webs supported along both vertical and horizontal axes. In contrast, the frame threads of webs on fences were usually attached only to upper and lower fence railings with no lateral support, resulting in webs with tension derived solely from the top and bottom (Fig. 2). While speculative, supporting webs along two axes rather than one may improve function in mechanical systems such as orb webs that must distribute the energy from impacts of flying prey and wind (Vollrath 1992; Lin et al. 1995). In other words, spiders may have reacted to the better support available to webs in laboratory cages by reducing the total number of radii in webs, while still maintaining the same effective degree of overall stiffness and function. Cage webs were elongated vertically (web asymmetry = 0.1) while fence webs were wider than tall (web asymmetry = −0.3). This shape is unusual for orb webs, but fence spiders expended relatively large volumes of silk into webs that had to

fit between the available fence rails. Therefore, they expanded laterally and ultimately produced capture areas similar to cage webs. This is similar to a study on *A. diadematus* where orb-web shape changed to optimally fill the space available in small, irregularly shaped cages, but only after overall web size was drastically reduced (Krink & Vollrath 1997, 2000). This suggests that spiders do have the capacity to assess the microhabitat available for webs and subsequently adjust the shapes of webs to maintain or maximize overall sizes.

Most research on orb-web function primarily focuses on changes in the shapes of webs and lengths of threads. However, there is growing evidence that spiders actively vary the diameters of silk threads within and between webs (Blackledge et al. 2005; Blackledge & Zevenbergen 2007; Boutry & Blackledge 2008). In general spiders increase silk diameter with body size, particularly given the role of draglines in suspending falling and hanging spiders (Brand-wood 1985; Osaki 1996; Ortlepp & Gosline 2008). Some spiders even control silk diameter in response to different types of prey (Boutry & Blackledge 2008). The cross-sectional areas of silk threads directly influence important mechanical properties such as the total loading and energy-absorbing capabilities of webs. In our study the greater volume of radial (MA) silk was driven primarily by the 50% greater cross-sectional areas of radii in fence webs, which would greatly increase the kinetic energy these webs could absorb from wind and prey impacts. In contrast, the cross-sectional areas of capture spirals were relatively similar between laboratory and fence webs, although the total length of the capture spiral was 42% shorter in cage webs.

In summary, we found that caged spiders in the laboratory invested less material in their webs than did fence spiders in the field. Several factors may explain the lower investment in webs by cage spiders: 1) spiders may first test foraging sites before building more substantial webs in new locations (Riechert & Gillespie 1986; Nakata & Ushimaru 1999); 2) caged spiders were exposed to fewer insect cues, such as wing vibrations and odor, and may have altered web spinning in response to perceptions of a poor foraging environment (Pasquet et al. 1994 Nakata & Ushimaru 2004); 3) the stiff supports of the laboratory cages provided structures on which mechanically effective webs could be built using less material (Wirth & Barth 1992) and reduced investment may reflect loss of silk resources when a spider is removed from its old web in the field without being allowed to recycle the silk (Zschokke 1997). Our study was not intended to distinguish among these factors, but only to determine the general effects of captivity on spider webs. Controlling for such factors in future studies of orb spinning could reveal the relative importance of each for spider behavior. Regardless, our study is consistent with the growing body of evidence that spiders modulate web-spinning behaviors in response to changing environments.

ACKNOWLEDGMENTS

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